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Automatic versus Choice-Dependent Value Representations in the Human Brain

Highlights

- Value representations in different brain regions serve distinct behavioral aims
- mPFC value coding is amplified when choices are based on values
- This enhancement of mPFC value signals is linked to choice consistency
- PCC value coding is automatic and relates to value-driven attentional capture

Authors

Marcus Grueschow, Rafael Polania, Todd A. Hare, Christian C. Ruff

Correspondence

marcus.grueschow@econ.uzh.ch (M.G.), christian.ruff@econ.uzh.ch (C.C.R.)

In Brief

Grueschow et al. report a functional dissociation in the human brain valuation system: activity in medial prefrontal cortex underlies goal-directed choices based on values, whereas neural signals in posterior cingulate cortex serve to attract attention to valuable, but unattended, items.

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Automatic versus Choice-Dependent Value Representations in the Human Brain

Marcus Grueschow,[1,*] Rafael Polania,[1] Todd A. Hare,[1] and Christian C. Ruff[1,*]
[1]Laboratory for Social and Neural Systems Research (SNS Lab), Department of Economics, University of Zurich, 8006 Zürich, Switzerland
*Correspondence: marcus.grueschow@econ.uzh.ch (M.G.), christian.ruff@econ.uzh.ch (C.C.R.)
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SUMMARY

The subjective values of choice options can impact on behavior in two fundamentally different types of situations: first, when people explicitly base their actions on such values, and second, when values attract attention despite being irrelevant for current behavior. Here we show with functional magnetic resonance imaging (fMRI) that these two behavioral functions of values are encoded in distinct regions of the human brain. In the medial prefrontal cortex, value-related activity is enhanced when subjective value becomes choice-relevant, and the magnitude of this increase relates directly to the outcome and reliability of the value-based choice. In contrast, activity in the posterior cingulate cortex represents values similarly when they are relevant or irrelevant for the present choice, and the strength of this representation predicts attentional capture by choice-irrelevant values. Our results suggest that distinct components of the brain's valuation network encode value in context-dependent manners that serve fundamentally different behavioral aims.

INTRODUCTION

Any decision based on personal preferences rests on the subjective value (SV) of the choice options, for example, when deciding which food to eat or whether to buy a product at a given price (Kahneman and Tversky, 1979; Rangel et al., 2008). Elucidating the neural mechanisms by which such SVs are represented is therefore paramount for understanding both healthy and maladaptive choice behavior (Bickel et al., 2007; Dixon et al., 2006; Leotti et al., 2010). To address this issue, numerous laboratory studies have correlated SVs during value-based choices with brain activity and have identified a valuation system comprising several regions, including the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC), and the ventral striatum (VS) (for recent meta-analyses see Bartra et al., 2013; Clithero and Rangel, 2014). Critically, these studies have typically examined value representations during choices in which the goal is to maximize the personal benefit of the agent and which are therefore taken based on the SVs (anticipated reward and costs) of the choice options. In these situations, participants naturally focus their attention on the choice-relevant SVs.

However, there is growing evidence that SVs can also influence behavior when they are currently choice-irrelevant and therefore outside the focus of attention (Della Libera and Chelazzi, 2006; Hickey et al., 2011; Theeuwes and Belopolsky, 2012). More specifically, the presence of a task-irrelevant item that was previously coupled with a reward can slow down performance of purely perceptual decisions performed on non-value-related stimulus dimensions (Anderson, 2013; Awh et al., 2012). This phenomenon—termed value-based attentional capture—is thought to reflect a brain mechanism that constantly monitors the environment for behaviorally relevant stimuli that may warrant a new course of action (Anderson, 2013; Pearson et al., 2011). This mechanism may allow the agent to notice valuable unattended alternative stimuli and enable behavioral engagement when this is beneficial.

Very little is known about how task-irrelevant SVs are represented in the brain and how they may exert their influence on behavior. Only few studies have examined correlations of brain activity with choice-irrelevant SVs, but crucially, the relationship between these signals and the behavioral slowing of non-value-based choices has not yet been established. This is primarily due to the fact that automatic or task-irrelevant SV signals have been investigated with paradigms that involved no choice at all (Levy et al., 2011), forced actions (Plassmann et al., 2007), or hypothetical choices (Tusche et al., 2010), thereby precluding quantitative assessment of how choice-irrelevant SVs impact on task performance during value-unrelated decisions. Moreover, it is an open question whether any such automatic SV representations are functionally overlapping with, or distinct from, choice-dependent SV signals, as previous studies that have assessed automatic SV coding during value-unrelated tasks have either focused on only one region (Kim et al., 2007) or have pooled activity across several brain areas (Lebreton et al., 2009). Thus, it is unclear whether different regions of the brain's valuation circuitry contain functionally distinct SV representations that differentially relate to value-based choices or value-based attentional capture.

To address this issue, we developed a choice task in which human participants alternated between purchasing decisions (for which SVs are directly choice-relevant) or perceptual decisions (for which SVs are unrelated to the current choice). Both types of choices were taken based on identical visual stimuli and motor responses. This paradigm is ideally suited for various hypothesis tests that can identify brain regions where SV representations predominantly relate to value-based choices or to value-based attentional capture.

First, we hypothesize that if a brain region specifically represents choice-relevant SV, then value coding should be enhanced in the context of purchasing compared to perceptual choices. This prediction stems from the well-documented effect that directing attention toward a specific stimulus feature enhances the sensitivity of visual neurons selective for that feature, typically by sharpening the neuronal tuning curve (Knudsen, 2007; Martinez-Trujillo and Treue, 2004; Reynolds and Chelazzi, 2004; Spitzer et al., 1988). This mechanism is thought to strengthen the neuronal representation of task-relevant features relative to background activity, thereby improving the signal-to-noise ratio and increasing the reliability of the neural signal used to control behavior (Kastner et al., 1999; Martinez-Trujillo and Treue, 2004; Moran and Desimone, 1985; Reynolds et al., 2000). We thus hypothesize that a similar mechanism may boost neural SV representations when these become choice-relevant. Any region in the brain representing predominantly choice-relevant SVs should exhibit a significantly steeper slope of the regression of neural activity on increasing SVs during purchasing compared to perceptual choices.

Second, we expect that these enhancements of neural SV representations are a critical determinant of the choice outcome. In general, attention-related activity modulations in functionally specialized regions are thought to result in higher reliability of the choice-relevant signals, thereby decreasing trial-to-trial variability of behavior for any constant stimulus (Desimone and Duncan, 1995; Knudsen, 2007; Luck et al., 1997). Thus, we hypothesize that the strength of the increase in SV representations during purchasing choices compared to the perceptual task will correlate with higher SV consistency across choices. SV consistency in this context means that if an item A is assigned a higher value than monetary amount X on a first occasion, then item A is also assigned a value higher than X when evaluated at a later time point (Rangel et al., 2008). In addition, we expect based on previous findings (Knutson et al., 2007) that regions implementing choice-relevant SV representations should contain signals that predict the actual purchasing choice.

In contrast to these hypotheses about choice-relevant SV representations, we expect that brain activity in regions representing SVs automatically (i.e., even when these are choice-irrelevant) will show a constant relationship to SVs for both purchasing and perceptual choices. This is because such regions encode SVs of potential choice options without being affected by the current task, and therefore in a similar fashion for both types of decisions (Kim et al., 2007; Lebreton et al., 2009). However, the strength of this automatic SV-related activity should relate to the degree of value-driven attentional capture for perceptual choices. That is, we expect that the strength of neural activity in any region representing SVs in an automatic fashion should correlate with the reaction time (RT) slowing observed during perceptual choices. This effect is thought to reflect that these neural SV representations automatically capture attention and therefore systematically slow down the unrelated perceptual choice (Anderson et al., 2011; Awh et al., 2012).

We directly tested these hypotheses for all putative valuation regions of the human brain, using fMRI in a sample of 26 healthy volunteers who took purchasing or perceptual choices on identical visual stimuli. This allowed us to measure and compare the neural response profiles for SVs when these were choice-relevant (during purchasing choices) or unrelated to the present decision (for perceptual choices). Moreover, we could directly relate the strength of these two types of value representations to SV consistency and choice outcome for value-based choices, or to value-based attentional capture during perceptual choices.

RESULTS

Behavioral Results

Both types of decisions were based on the same visual stimuli (DVD movie covers, each presented only once per decision type; Figures 1A and 1B) and were carefully matched for identical motor responses and RTs (Figures 1D–1F). RTs in both tasks did not significantly differ ($t_{25} = -0.17$, $p = 0.86$, paired t test; Figures 1D and 1E) but were strongly correlated across participants, indicating that both types of choices did not entail fundamentally different processing demands ($r = 0.82$, $p < 0.001$; Figure 1F). SV for each movie was quantified by willingness-to-pay ratings (Becker et al., 1964) (between 0 and 20 Swiss francs for 672 movies)—a standard method widely used in behavioral economics and neuroeconomics (Krajbich et al., 2010; Plassmann et al., 2007)—which were provided by each participant 1–3 days prior to fMRI.

During scanning, SVs were directly relevant for the purchasing decisions, which required the participants to choose whether or not to buy the depicted movie at an aurally presented price that varied around the predetermined SV. In contrast, SVs were irrelevant for the matched perceptual decisions (Polanía et al., 2014), in which participants judged whether the numbers of faces (FV) present on the DVD cover matched an aurally presented number that varied around the actual FV (see Experimental Procedures for details). Importantly, SV and FV were uncorrelated in both tasks ($t_{25} = -1.34$, $p = 0.19$; Figure 1C), therefore allowing unbiased analyses of how SVs are neurally represented during both types of choices.

We confirmed that SV was indeed choice-relevant for purchasing decisions and choice-irrelevant for perceptual decisions using multiple logistic regression analyses of participants' behavioral responses. This showed that the difference between SV and the aurally presented price strongly affected accept/reject purchasing choices ($t_{25} = 9.24$, $p = 1.5 \times 10^{-9}$; Figure 2A; one-sample t test; see Experimental Procedures), but not perceptual choices ($t_{25} = -1.62$, $p = 0.12$; Figure 2B). Conversely, the absolute difference between FV and the aurally presented number strongly affected perceptual choices ($t_{25} = -16.03$, $p = 1.1 \times 10^{-14}$; Figure 2B), but not purchasing choices ($t_{25} = 1.37$, $p = 0.18$; Figure 2A). These analyses thus confirm that participants indeed based their choices exclusively on SVs for value-based choices and on FVs for perceptual decisions.

To test whether our data also exhibit the predicted value-driven attentional capture effect (i.e., slowing of perceptual choices with increasing choice-irrelevant SV) (Anderson et al., 2011), we regressed RTs of perceptual decisions on the trial-wise SV and FV (Figure 2D). Unsurprisingly, we found that RTs increased with an increasing number of faces participants had to match (FV; $t_{25} = 14.35$, $p = 1.4 \times 10^{-13}$), but crucially, we also found a significant RT increase proportional to the

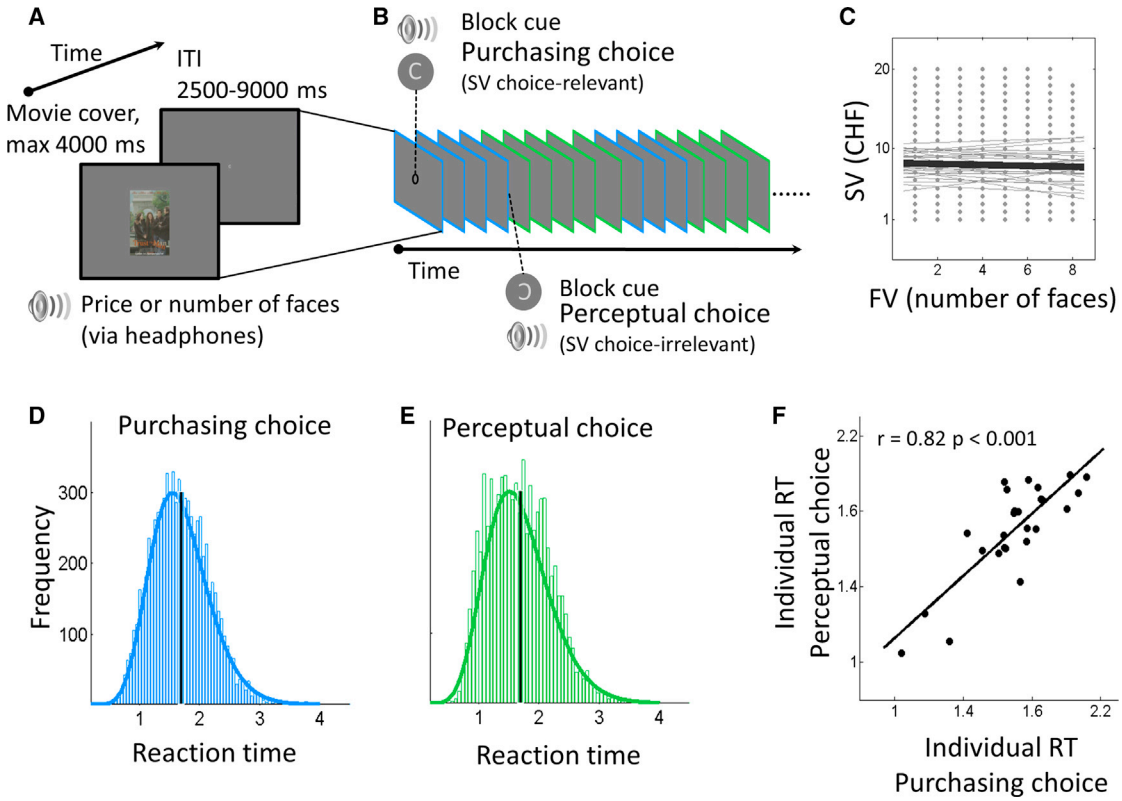

Figure 1. Experimental Task and Reaction Time Results

(A) In the scanner, participants performed two types of choices on identical DVD cover stimuli (see also Experimental Procedures for details). For value-based choices (SV choice-relevant), participants indicated their willingness to pay a specified price for that movie under real purchasing conditions. For perceptual choices (SV choice-irrelevant), participants indicated whether the aurally presented number of faces matched the number of faces on the cover.

(B) Purchasing and perceptual choices were presented in randomly alternating mini-blocks of 3–5 trials each. The choice type was indicated prior to each block via an auditory cue. During each block, the choice type was furthermore indicated by a central visual marker (C for purchasing decisions and rotated C for perceptual decisions). Each movie cover was presented only once for purchasing and perceptual choices, respectively, in a randomized order to counteract possible novelty or memory effects.

(C) SV and FV were uncorrelated in both tasks (mean $\beta = -0.234$, linear regression, $t_{25} = -1.3398$, $p = 0.1924$, one-sample t test). Gray lines represent single-subject regressions of FV on SV. Thick black line represents this regression across subjects. Gray dots indicate SV/FV combinations that occurred at least once during the experiment.

(D and E) Reaction time distributions for purchasing choices (SV choice-relevant) and for perceptual decisions (SV choice-irrelevant). Bars represent observed counts, and smooth lines represent gamma probability density functions fitted to the underlying distributions using maximum-likelihood estimation. Vertical black lines represent the reaction time means, which were not significantly different (purchasing decisions = 1.694 s, perceptual decisions = 1.7 s; $t_{25} = -0.17$, $p = 0.86$, paired t test).

(F) Individual mean RTs were strongly correlated between both types of choices, indicating that both types of choices did not entail fundamentally different processing demands.

choice-irrelevant SVs of the DVDs ($t_{25} = 3.66$, $p = 1.2 \times 10^{-3}$). This confirms that a value-driven attentional capture mechanism is engaged during perceptual choices. The speed of purchasing decisions was also affected by choice-relevant SV ($t_{25} = 2.22$, $p = 0.036$; Figure 2C), but not by the number of faces on the cover ($t_{25} = 0.76$, $p = 0.45$; Figure 2C), thereby further confirming that participants were only affected by SVs (and not FVs) when taking value-based choices.

Functional Imaging Results

The primary aim of the fMRI analyses was to compare how automatic and choice-dependent value representations are implemented in the human brain. To this end, we took great care to ensure that experimental stimulation (visual/auditory), RTs, and motor responses were identical across both types of choices. This precise match in sensory and motor-related neural processing between both types of decisions was reflected in the substantial overlap of blood oxygen level-dependent (BOLD) activity in audio-, visual-, and motor-associated regions common to both types of choices (conjunction analysis all $p < 0.05$, FWE-corrected; Figure 3A; see Table S1). Nevertheless, purchasing and perceptual choices strongly differed in how they recruited value-related or perceptual processing: when comparing mean BOLD activity between both types of choices (averaging across all levels of SV and FV), we found regions routinely associated with subjective valuation (such as the mPFC and PCC; see Bartra

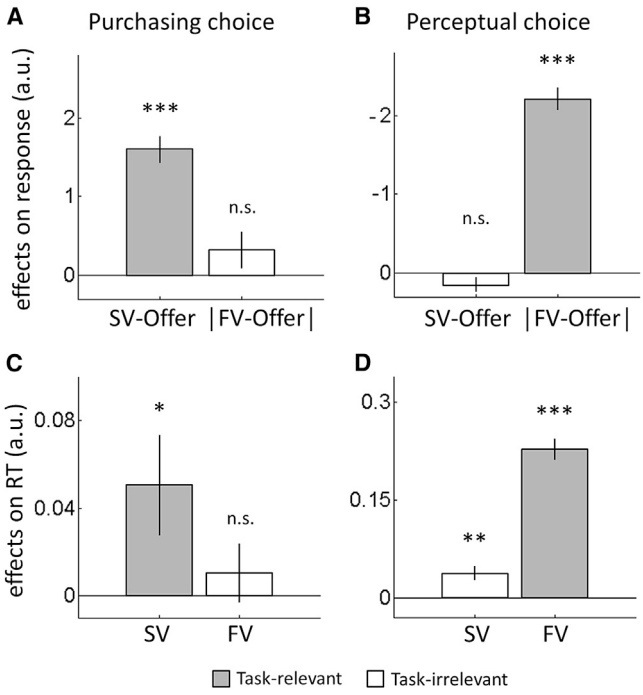

Figure 2. Behavioral Results

The trial-wise SVs were directly relevant for the participant's purchasing decisions, but irrelevant for the matched perceptual decisions.

(A and B) During purchasing trials, decisions to accept or reject depended positively on the difference between SV and the aurally presented price (multiple logistic regression; t_{25} = 9.24, p = 1.5 × 10^{-9}), while this index was irrelevant for perceptual choices (t_{25} = 1.37, p = 0.18). This regression indicates that the higher the difference between SV and offer price (consumer surplus), the more likely a purchase response.

During perceptual trials, responses depended negatively on the absolute difference between the number of faces (FV) and the aurally presented number (t_{25} = −16.03, p = 1.2 × 10^{-14}), while this index was irrelevant during purchasing choices (t_{25} = 1.62, p = 0.12). This regression indicates that the higher the absolute difference between FV and the offered criterion, the less likely an accept response. Please note that the y scale in (B) has been inverted to facilitate illustration and visual comparison with the other panels.

(C) RTs during purchasing decisions were significantly affected by the task-relevant SV (t_{25} = 2.22, p = 0.036), while the number of faces on the cover had no effect (t_{25} = 0.76, p = 0.45) on RTs.

(D) RTs during perceptual choices were slowed down by task-relevant FV (t_{25} = 14.3517, p = 1.4 × 10^{-13}), and crucially, also by task-irrelevant SV (t_{25} = 3.66, p = 0.00117), thereby confirming value-based attentional capture. Error bars in all panels represent ± 1 SEM (n = 26).

et al., 2013; Clithero and Rangel, 2014) significantly more activated during purchasing decisions than during perceptual decisions, whereas regions of the so-called dorsal attention network (i.e., inferior parietal sulcus [IPS], frontal eye fields [FEFs]; see Corbetta et al., 1991; Corbetta and Shulman, 2002) as well as the lateral occipital complex (LOC) were significantly more activated during perceptual as compared to purchasing choices (all p < 0.05, FWE-corrected; Figure 3B; see Table S2). These results confirm that despite their identical sensory and motor demands, the two types of decisions in our paradigm flexibly recruited regions that are functionally specialized for processing the information relevant for the current choice.

Two Distinct Types of Value Representations in the Brain

To distinguish choice-related versus automatic value computations in the human brain, we tested for neural activity that either represented SVs predominantly when these were task-relevant or that coded value irrespective of current behavioral goals. For this purpose, we regressed BOLD signals against the trial-wise SV of the DVDs during purchasing decisions—when the choice strongly depended on SV—and during perceptual decisions, in which SVs were irrelevant for the current choice. This analysis revealed that both types of SV representations are encoded in the brain, but in clearly dissociated regions of the valuation system. On the one hand, BOLD signals in mPFC (Figures 4A, 4C, 4E, and 4G) and bilateral VS (Figure S1; Table S3) significantly correlated with SVs during purchasing decisions, but not during perceptual decisions, suggesting that both these regions mainly represent values when these are choice-relevant. Importantly, a direct contrast between purchasing and perceptual decisions confirmed that activity in both mPFC and VS showed significantly stronger correlations with SVs during purchasing decisions compared to perceptual decisions (Figures 4C, 4E, 4G, and S1B–S1D). We also note that this BOLD signal enhancement during purchasing choices was indeed related to the SVs of the DVDs and did not reflect the varying levels of prices presented alongside the items (see Supplemental Results for the relevant control analyses).

In contrast to mPFC and VS, BOLD signals in the PCC (Figures 4B, 4D, 4F, and 4H) showed similar positive correlations with both choice-relevant SV during purchasing decisions and choice-irrelevant SV during perceptual decisions. Note that correlations with SV during perceptual choices were also found for other areas such as bilateral dorsolateral prefrontal cortex (dlPFC) and bilateral parietal lobule (Figure S2; Table S3). This may possibly index a function of these areas in the filtering of distracting stimuli during perceptual choice (Friedman-Hill et al., 2003; Lennert and Martinez-Trujillo, 2011). However, the PCC was the only region that represented SVs both when these were relevant and irrelevant for the current decision (Figures 4D, 4F, and 4H), thereby fulfilling our requirements for an area that contains truly automatic, choice-independent value representations.

Our data therefore demonstrate a functional dissociation between brain regions consistently linked to value processing (Bartra et al., 2013; Clithero and Rangel, 2014). While the PCC represents SV in an automatic fashion that is invariant to current behavioral aims, the mPFC and VS represent SV predominantly when it is relevant for the current choice.

mPFC Activity Relates to Value-Based Choice Consistency

We next tested whether the strength of the choice-dependent SV representations related to the behavioral consistency of value-based choices. Consistency here refers to how well the participants' choices in the scanner agreed with their Becker-DeGroot-Marshak (BDM) auction rating for each DVD provided 1–3 days prior to scanning (Becker et al., 1964; Krajbich et al., 2010; Plassmann et al., 2007). That is, a choice is SV-consistent

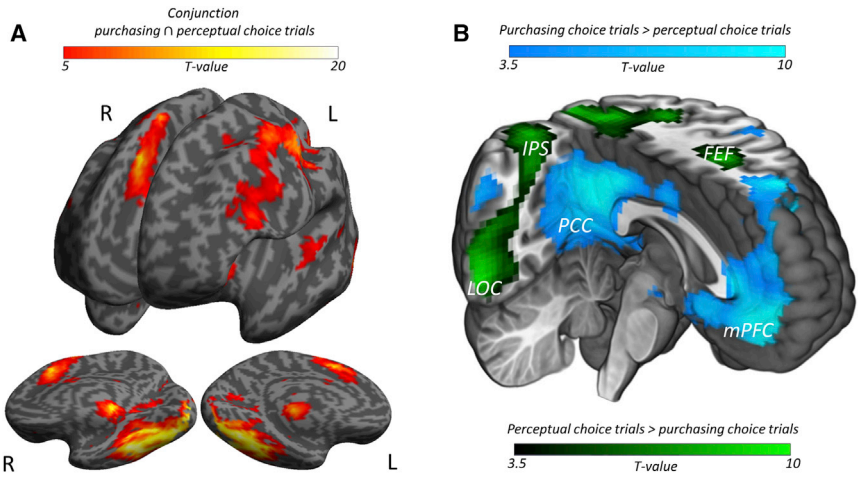

Figure 3. Average Brain Activity that Is Common and Distinct for Both Types of Choice

(A) Common decision-related activity in both tasks (conjunction at $p < 0.05$, FWE cluster-corrected, see Table S1 for complete list) was found in the ventral visual stream along the fusiform gyrus, in subcortical visual areas such as the lateral geniculate nucleus, and in the auditory cortex along the bilateral superior temporal gyrus. In addition, we found regions associated with motor responses—such as the SMA, pre-SMA, and the left motor cortex—to be similarly engaged in both tasks. SMA, supplementary motor area.

(B) Comparison of average decision-related activity (not parametric modulation by SV) between both types of choice revealed distinct activations for purchasing and perceptual choices. Blue represents significant activity for purchasing > perceptual choices, whereas green represents significant activity for perceptual > purchasing choices (see Table S2) (both at $p < 0.05$, FWE cluster-corrected).

if participants purchase a DVD when its price is less than or equal to the value they stated previously, or if they decline to purchase a DVD when its price is above their previously stated value. We expected a relation between SV consistency and neural SV representations because stronger neural choice-relevant value responses result in an enhanced signal-to-noise ratio and thus more reliable behavioral readout of the values across both testing occasions. We tested for such a consistency effect with a linear mixed-effects regression of the proportion of consistent choices on the average strength of the neural choice-relevant value responses (this analysis was conducted across value quintiles, see Experimental Procedures for details). Note that the data submitted to these analyses were extracted from regions of interest that were independently defined by the leave-one-subject-out (LOSO) procedure to avoid circularity (Esterman et al., 2010; Kriegeskorte et al., 2009; Poldrack and Mumford, 2009; see Experimental Procedures for details).

Only the mPFC showed a relationship between the magnitude of BOLD response and choice consistency ($X^2 = 4.85$, $p = 0.027$, likelihood ratio test), while no such relationship was found for PCC ($X^2 = 0.23$, $p = 0.629$), and only a trend emerged for VS ($X^2 = 2.43$, $p = 0.12$) (Figure 5A; Table S5). Importantly, the strength of value-related BOLD activity in the mPFC was more strongly related to choice consistency than the corresponding PCC activity ($X^2 = 6.49$, $p = 0.01$, likelihood ratio test; Table S5), suggesting that the value signals in mPFC are more relevant for purchasing behavior than SV signals from task-invariant PCC. The data regarding stronger involvement of the VS as compared to PCC are inconclusive, as they revealed only an effect at trend level ($X^2 = 2.38$, $p = 0.13$).

We also tested whether SV consistency was specifically related to the strength of the choice-related enhancement of value coding in mPFC. That value-based consistency is not driven purely by behavioral SVs (but rather by their neural representation) is already evident from the finding that during purchasing choices, SV consistency was selectively related to value coding in the mPFC, but not in the PCC. If the choice-related enhancement of mPFC value responses indeed increases the fidelity of value coding, then SV consistency should relate to the strength of the difference between the choice-relevant and choice-irrelevant value response profile. We again tested this hypothesis with linear mixed-effects analyses (see Experimental Procedures for details). This revealed a significant relationship only in the mPFC ($X^2 = 4.12$, $p = 0.042$, likelihood ratio test), but not in PCC ($X^2 = 0.36$, $p = 0.55$) or VS ($X^2 = 0.01$, $p = 0.94$). Crucially, the value signal enhancement in mPFC accounted for value-based consistency significantly better than the corresponding enhancement in the PCC ($X^2 = 3.78$, $p = 0.05$) or the VS ($X^2 = 4.95$, $p = 0.026$). Thus, these findings suggest that the enhancement of value representations in the mPFC during purchasing decisions specifically increases the stability of these representations and thereby leads to more consistent value-based choices.

Relating Neural Signals to Purchasing Choices

Previous studies (Knutson et al., 2007; Padoa-Schioppa, 2013; Strait et al., 2014) have shown that valuation regions contain signals that can be used to predict choice outcomes. We therefore expected that regions containing choice-relevant SV signals should—in addition to supporting consistent valuation of items across decision contexts—also provide information about whether or not a DVD will be purchased in our task. We tested this hypothesis with analyses of how purchasing decisions on any given trial can be predicted by BOLD activity in the mPFC, VS, and PCC. To this end, we performed a receiver operating characteristic (ROC) analysis (Green and Swets, 1966) that quantifies the reliability with which the single-trial amplitude of the BOLD signal—at various time points following stimulus onset—predicts the purchasing choice on that trial (see Experimental Procedures for details). Consistent with previous reports (Knutson et al., 2007), we found that BOLD signals in the mPFC within 4–8 s post-stimulus significantly predicted purchases, while the corresponding signals extracted from PCC did not (Figure 5B). The response timing of this relationship was similar to the peak delay and temporal spread of the hemodynamic response following trial onset,

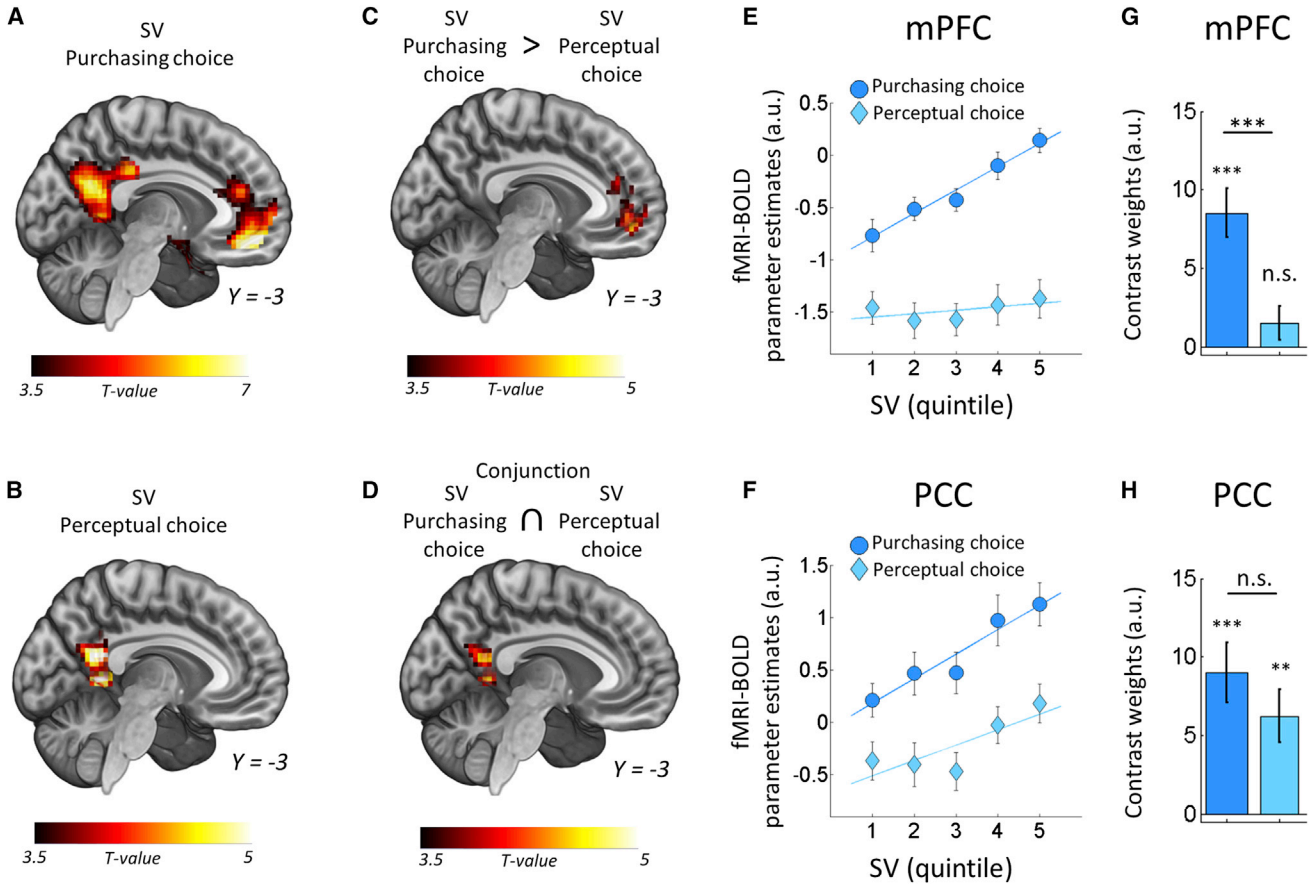

Figure 4. Distinct SV Representations in mPFC and PCC

(A) Choice-relevant SV during purchasing decisions correlates with BOLD signals in mPFC and PCC (see also Figure S1 for SV representations in the ventral striatum).

(B) Choice-irrelevant SV during perceptual decisions correlates with BOLD signals in PCC, bilateral dlPFC, and bilateral parietal lobule (see Figure S2 and Table S3 for statistics and peak coordinates).

(C) A direct comparison of SV representations during purchasing choices versus SV representations during perceptual choices reveals a slope increase when SV is choice-relevant (during purchasing choices) in mPFC (peak $t_{25} = 4.72$, x = −3, y = 50, z = −11, p = 0.05, FWE cluster-corrected). This effect is visualized in (E) by the parameter estimates extracted from 5-mm spheres centered on peak voxels of the choice-relevant SV > choice-irrelevant SV contrast, determined by the leave-one-subject-out procedure to ensure independence (Experimental Procedures).

(D) A conjunction analysis between SV representations during purchasing choices and perceptual choices reveals a task-invariant SV representation in PCC (conjunction, peak $t_{25} = 5.04$, x = −6, y = −52, z = 19, p < 0.05, FWE cluster-corrected). This effect is visualized in (F) by the parameter estimates extracted from 5-mm spheres centered on peak voxels of the choice-irrelevant SV contrast, as determined by the leave-one-subject-out procedure.

(G) and (H) visualize and quantify the slopes of the choice-relevant (dark blue) and choice-irrelevant (light blue) SV representation in mPFC and PCC, respectively. The panels plot the contrast weights from the same 5-mm spheres as in (E) and (F), respectively. BOLD activity in both mPFC ($t_{25} = 5.26$, $p = 1.8 \times 10^{-5}$) and PCC ($t_{25} = 4.64$, $p = 9.4 \times 10^{-5}$) significantly increases with increasing task-relevant SV, but only activity in PCC also significantly increases with increasing task-irrelevant SVs ($t_{25} = 3.66$, $p = 1.2 \times 10^{-3}$). In direct comparisons, the slope of the task-relevant SV representation in mPFC is significantly increased compared to the task-irrelevant SV representation ($t_{25} = 4.30$, $p = 2.3 \times 10^{-4}$), whereas no such difference could be observed for PCC ($t_{25} = 1.32$, p = 0.1974). Error bars in all panels represent ± 1 SEM (n = 26). Please see also Figure S4 and Table S4 for FV representations.

suggesting that the mPFC activity that predicts purchases is associated with the decision period lasting for about 1.7 s. Importantly, within the time period between 4 and 8 s after stimulus onset, the mPFC predicted purchases significantly better than the PCC (paired t tests, p < 0.05, two-tailed; Figure 5B). Note that we did not find purchasing-predictive activity in the VS (see Figure S3), again in line with previous reports examining similar fixed-price purchasing decisions as employed here (Knutson et al., 2007).

PCC Activity Relates to Value-Driven Attentional Capture

The BOLD signal response profile observed in the PCC suggests that this region is involved in automatic value coding, as it exhibits context-invariant value representations that are similar during purchasing and perceptual decisions. We therefore examined whether the choice-irrelevant value representations during perceptual decisions reflect automatic SV computations that may facilitate attentional orienting to valuable

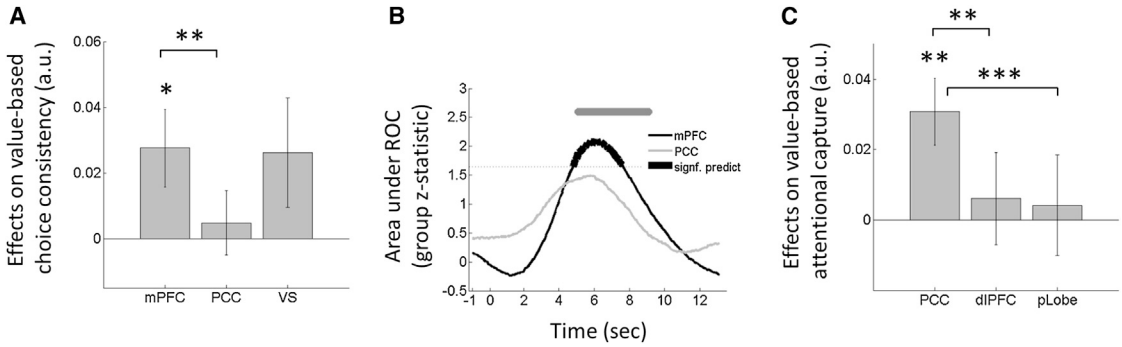

Figure 5. Relating Neural Activity to Behavior

(A) Value representations in mPFC, but not PCC, relate to choice consistency. The plot shows standardized estimates from multiple regressions of choice consistency on SV-related BOLD signals in different regions. BOLD signals in mPFC (X^2 = 4.85, p = 0.027, likelihood ratio test) relate to choice consistency during purchasing decisions, whereas the corresponding signals in PCC (X^2 = 0.23, p = 0.629) do not (see Table S5). The same analyses for the VS reveal an effect at trend level (X^2 = 2.43, p = 0.12). Importantly, the mPFC effects are significantly stronger than the corresponding effects for PCC (p = 0.01). Please see Experimental Procedures for details on regressions and model comparison.

(B) Neural activity in mPFC, but not PCC, can predict purchases. The plot shows the time course of purchase-predictive activity estimated as the area under the *Z*-transformed ROC curve. BOLD signals in mPFC (black line) predict purchases significantly above chance (gray dotted horizontal line represents the one-tailed group *Z* statistic critical value z = 1.64) approximately 4–8 s after stimulus onset (thick black line), whereas PCC responses do not predict purchases at any time point (gray line). Additionally, mPFC signals predict participants' purchases significantly better than PCC signals during the time period indicated by the thick gray bar after stimulus onset (paired t tests, p < 0.05). Please see Experimental Procedures for details on the ROC analysis and Figure S3 for ventral striatum results.

(C) Value representations in PCC relate to value-driven attentional capture. The plot shows standardized estimates from multiple regressions of value-based attentional capture on value-related BOLD signals from all regions identified as showing task-irrelevant SV representations. Neural activity in PCC shows a strong relationship (X^2 = 9.83, p = 1.7 × 10^{-3}) with the RT slowing due to task-irrelevant SV during perceptual decisions, while dlPFC (X^2 = 0.21, p = 0.65) and parietal lobule (X^2 = 0.08, p = 0.78) do not (see Table S6). Error bars in all panels represent ± 1 SEM (n = 26). Please see Experimental Procedures for details on regressions and model comparison.

items outside the current focus of attention. To this end, we tested whether the strength of choice-irrelevant SV representations during perceptual decisions related to the degree of value-based attentional capture, i.e., the behaviorally observed RT slowing of perceptual choices with increasing SVs (Anderson et al., 2011). We tested this hypothesis for all three regions that were found to represent choice-irrelevant SVs (PCC, dlPFC, and parietal lobule) using linear mixed-effects analyses (again, these analyses were performed on data binned into SV quintiles, see Experimental Procedures). Only signals in the PCC showed the predicted significant relationship between perceptual RTs and choice-irrelevant SV response strength (X^2 = 9.83, p < 0.002, likelihood ratio test) (Table S6). Additionally, PCC value signals accounted for this effect more strongly than corresponding signals in the dlPFC (X^2 = 10.27, p = 0.001) and parietal lobule (X^2 = 11.45, p = 7 × 10^{-3}) (Table S6). For completeness, we also compared the strength of this relationship between the PCC and the mPFC and VS, even though the latter two regions did not actually contain any significant SV representations during perceptual choices (see above). This confirmed that choice-irrelevant SV signals from PCC explained the degree of value-based attentional capture significantly better than the corresponding activity in mPFC (X^2 = 5.74, p = 0.016) and VS (X^2 = 9.08, p = 0.003). These results demonstrate that the strength of automatic neural SV representations in the PCC directly relates to the degree to which choice-irrelevant SVs slow down perceptual performance, consistent with the idea that these PCC signals are involved in value-based attentional capture during perceptual choices.

DISCUSSION

Our study identified two distinct types of value-coding mechanisms in the human brain, by comparing value representations and their relation to behavior during two choice situations in which SVs were either relevant or unrelated to the present choice. Our results revealed a clear functional dissociation between different regions of the human brain's valuation circuitry. SV representations in the mPFC were enhanced when SVs became choice-relevant, and the strength of this enhancement related to the consistency and outcomes of choices. In contrast, SV representations in the PCC were invariant across contexts and related to value-driven attentional capture when SVs were irrelevant for the choice.

The sharpening of SV response profiles in mPFC and VS may reflect behaviorally relevant increases in signal-to-noise ratio similar to the sharpening of neuronal tuning curves associated with attention that lead to enhanced perceptual sensitivity (Knudsen, 2007; Martinez-Trujillo and Treue, 2004; Reynolds and Chelazzi, 2004; Spitzer et al., 1988). This sharpening process may provide a mechanistic explanation for recent findings that attention can change value-based choices and related neural activity. For instance, fMRI activity in the mPFC can increase when participants direct attention to the affective value (versus perceptual intensity) of a stimulus (Rolls and Grabenhorst, 2008) (cf. Figure 3B). Moreover, visual fixations on an item from a choice set are associated with a higher probability of choosing that item (Krajbich et al., 2010) and can determine whether its SV impacts negatively or positively on neural activity in the mPFC and VS (Lim et al., 2011).

Furthermore, computational models that include attentional modulation of the relative model inputs account better for several aspects of value-based choice behavior than models that do not incorporate attention or fixation patterns (Krajbich et al., 2012; Towal et al., 2013). Finally, non-human primates with mPFC lesions exhibit deficits in focusing on the most relevant comparison in a three-option task (Noonan et al., 2010), and addition of a third choice option changes mPFC value signals and choices between two constant stimuli (Chau et al., 2014).

While all these previous findings suggest that attention-related mechanisms can influence value-based choices and SV-related BOLD signals, our study clearly demonstrates that attention to a single item's SV leads to an enhancement of its value representation in the mPFC, and this signal enhancement directly relates to the consistency and outcome of purchasing choices. These effects may provide a value-based analog to effects of covert attention on perception and corresponding neural modulations observed in visual cortex (Reynolds and Heeger, 2009), which are thought to improve the fidelity of the neural signal and thereby the reliability of the choice-relevant information (Desimone and Duncan, 1995; Kastner et al., 1999; Knudsen, 2007; Luck et al., 1997; Martinez-Trujillo and Treue, 2004; Moran and Desimone, 1985; Reynolds et al., 2000). Please note in this context that the observed task-related modulations of SV coding were clearly distinct from corresponding effects on FV representations relevant for the perceptual choices: contrasting choice-relevant and choice-irrelevant FV effects for perceptual choices (Table S4) revealed activation in parietal cortex and FEFs, just as one would predict based on studies comparing active attention conditions to passive fixation (Figure S4) (Culham et al., 2001; Kanwisher and Wojciulik, 2000).

Our findings also have bearings on previous studies investigating choice-relevant and choice-irrelevant SV representations with seemingly contradictory results (Lebreton et al., 2009; Plassmann et al., 2007). Lebreton et al. described the ventromedial PFC as part of a multi-region brain valuation system that shows automatic choice-irrelevant SV coding, whereas Plassmann et al. find this region to correlate stronger with SV in free (SV-relevant) than in forced (SV-irrelevant) value-based choices. These conflicting conclusions may reflect differences in analysis methodology. While Plassmann et al. performed a whole-brain voxel-wise analysis as employed by the present work, Lebreton et al. pooled activity across several regions (including mPFC, VS, and PCC), therefore precluding the possibility of region-specific inference. It is possible that the features of the automatic SV representations reported by Lebreton et al. are mainly driven by the PCC. Another possible explanation for the divergent findings relates to the nature of the behavioral paradigms. The non-value-related tasks used by Plassmann et al. and ourselves required an evaluation/action that could be objectively correct or wrong and that was fully unrelated to the item's value. In contrast, the SV-irrelevant task used by Lebreton and colleagues required the participants to subjectively evaluate the age of the stimulus in unspeeded choices, which may have triggered concomitant assessment of the items' SV (i.e., the age of a painting/house/person usually has implications for its value to an observer). Further studies may be required to fully resolve these inconsistencies.

We found that the strength of value-related activity in the PCC correlated with the degree by which RTs were slowed for perceptual decisions. These results suggest a crucial role for the PCC in automatic value coding and value-driven attentional capture. Our findings may thus have important implications for a large body of data on shifts of attention as studied with electroencephalography (EEG). The crucial scalp component associated with shifts of attention (N2pc) (Eimer, 1996) has consistently been attributed to parietal-occipital scalp sites (Luck and Hillyard, 1994; Woodman and Luck, 1999), including cases in which the targets were associated with higher, compared to lower, reward (Kiss et al., 2009). The precise neuroanatomical source for these effects, however, is difficult to locate with EEG. Our data suggest that the PCC may be a likely origin for the parietal-occipital N2pc component, at least in situations where previously unattended values of visual objects capture attention.

The automatic nature of SV representations in PCC may constitute an important evolutionary advantage, as it could ensure that SVs of external environmental features are continuously encoded with minimal use of attentional resources, in order to trigger behavioral engagement with alternative courses of action whenever this is beneficial. This proposed function is in line with recent findings that in volatile environments, macaque PCC neurons encode dynamic signals that are used for the decision to explore alternative actions in the future (Hayden et al., 2008). Moreover, our results also appear consistent with findings that macaque PCC neurons are involved in change detection and policy control during reward-guided behavior (Pearson et al., 2011), by contributing to the automatic detection of a superior option (based on prior experience or reward history) and the subsequent actions taken to either exploit or explore alternative options (Pearson et al., 2009). All these proposals support the view that the PCC may play a crucial role in optimizing reward-based behavioral control by evaluating alternative courses of actions (Heilbronner and Platt, 2013), and the neural computations necessary for this function may arrest or at least slow down current behavior as observed in value-based attentional capture.

We found two additional regions, bilateral dlPFC and bilateral parietal lobule, that coded irrelevant SV during perceptual choices. Both regions are part of a broader brain network involved in the control of cognitive functions such as working memory and spatial attention (Constantinidis and Procyk, 2004; Corbetta and Shulman, 2002; Todd and Marois, 2004). The two areas are tightly interconnected and share many functional properties, including a crucial role in maintaining a stimulus in working memory and filtering distracting stimuli (Katsuki and Constantinidis, 2012). Thus, it is possible that these two areas worked to counteract the automatic SV effects triggered by the PCC, by preventing the increasing interference of stimulus value with the perceptual task demands. This interpretation is consistent with the finding that the two regions only coded SVs during perceptual choices, but not when the SVs became choice-relevant during the purchasing decisions.

Taken together, our results demonstrate a fundamental functional dissociation between different brain regions whose contributions to reward representation and value-based choice have, thus far, been largely indistinguishable (Bartra et al., 2013; Clithero and Rangel, 2014). In the mPFC, SV representations reflect

a choice-dependent value-coding mechanism that is enhanced when SV becomes relevant for the decision at hand. These value-related neural responses in the mPFC carry information related to choice consistency and can be used to predict purchases. In the PCC, by contrast, SV representations are invariant across situations where SV is relevant or irrelevant for current behavior, and the strength of this automatic SV representation relates to value-driven attentional capture. The PCC may therefore play a crucial role in facilitating shifts of attention toward valuable items or actions outside the current focus of attention. The functional dissociation observed here suggests that disruptions of each of these two mechanisms will have distinct impacts on behavior. Direct comparisons of choice-dependent and automatic value coding in the brain may therefore help in diagnosing and potentially treating pathological disturbances of value-based behavioral control in the context of brain disorders such as addiction (Berridge, 2012; Davis, 2010; Field and Cox, 2008), attention deficit/hyperactivity disorder (Castellanos and Proal, 2012; Davis, 2010), and autism (Sasson et al., 2008, 2011).

EXPERIMENTAL PROCEDURES

Participants

A total of 26 subjects (20–28 years old; 13 males) provided informed consent as approved by the Research Ethics Committee of the Canton of Zurich. All subjects had normal or corrected-to-normal vision, were in good health, and reported no current use of medication as measured with standard surveys.

Rating Session

Between 1 and 3 days prior to functional imaging, subjects were given an allowance of CHF 20 and rated their willingness to pay (between 0 and 20 CHF) for each of 672 movies in a BDM auction (Becker et al., 1964). The optimal strategy in this setting was to truthfully indicate the SV of each movie (Krajbich et al., 2010; Plassmann et al., 2007). During each trial of the auction, the movie cover and title were presented for 1 s; the title remained on screen until the subject entered their SV via computer keyboard. Entered values were displayed on the screen and could be changed until the subject finalized their choice by pressing the enter key. Subjects were allowed to rate at their own speed, but every 100 trials short breaks were suggested. The rating lasted between 40 and 60 min.

fMRI Task

During the event-related fMRI sessions (Figures 1A and 1B), subjects took either purchasing or perceptual choices in randomly alternating blocks, thereby changing between choice settings in which SVs of the movie were choice-relevant (purchasing choices) or choice-irrelevant (perceptual choices). Both blocks were cued visually and aurally. For both types of decisions, participants viewed the same DVD covers, heard numbers via headphones, and indicated their choices via the same two response buttons. For purchasing decisions, subjects indicated whether the number represented an amount they were willing to pay for that movie (Plassmann et al., 2007). SV was therefore choice-relevant, because subjects had to evaluate whether their SV for the DVD was high enough to pay the stated price. For these trials, participants were endowed with an allowance of 20 CHF to spend, and one trial was randomly selected, and the decision on that trial was implemented after the experiment. During perceptual decisions, subjects indicated whether the presented number matched the number of faces on the cover. The SV of the DVD was therefore choice-irrelevant. This allowed us to assess and compare its representation between two contexts that differed in SV relevance, but that were matched in sensory input, motor response, and RT (Figures 1D–1F).

In order to encourage active engagement and attentional focus on the choice-relevant stimulus dimension (SV or number of faces [FV]), the covers were slightly phase-randomized as in Rieger et al., 2013, ensuring a perceptual accuracy level between 75% and 95% correct FV detections, as determined from pilot data on 21 subjects. For each purchasing choice, the auditory offer number was chosen from a uniform discrete distribution bracketing the SV (possible difference to SV: −4, −2, 0, +2, or +4 CHF). For perceptual choices, the number varied uniformly around the true number of faces (by −2, −1, 0, +1, or +2). We defined purchasing decisions as value-consistent if participants accepted auditory offers equal to or below the SV or rejected offers that were higher than the SV (all other choices were defined as value-inconsistent). The subject-specific SV values for the DVDs were determined prior to the choice task using the BDM auction procedure. Perceptual choices were defined as correct if participants accepted auditory offer numbers that matched the actual face number, whereas all other choices were incorrect (see Supplemental Experimental Procedures for further details).

Behavioral Analysis

To confirm that participants followed the task instructions and chose based on the difference between SVs and the price (for purchasing decisions) or the match between the perceptual criterion and the number of faces on the cover (for perceptual decisions), we regressed accept/reject choices in both tasks against (SV-Offer) and (|FV-Offer|) using within-subject multiple logistic regression with the formula below:

$$P_{accept} = \frac{1}{1 + \exp(-(\beta_0 + \beta_1(\text{SV-Offer}) + \beta_2(|\text{FV-Offer}|)))}$$

To test for attentional capture by choice-irrelevant SV during perceptual choices, we performed a within-subject multiple linear regression of RTs on each DVD's SV and FV (SV should result in a slowing of perceptual choices if it captures attention despite not being choice-relevant) with the formula below:

$$RT = \beta_0 + \beta_1 SV + \beta_2 FV$$

The resulting individual regression parameter estimates were standardized, and their significant deviance from zero was tested using a two-sided t test.

fMRI Data Analysis

Subjects performed ten choice-task sessions (each containing 30 purchasing and 30 perceptual choices) while being scanned with a Philips Achieva 3 T whole-body scanner (Philips Medical Systems). Image pre-processing and analysis were conducted using SPM8 (Wellcome Trust Centre for Neuroimaging). For more detailed information regarding fMRI data acquisition, pre-processing, and peripheral measures please see Supplemental Experimental Procedures.

We estimated five general linear models (GLMs). The main GLM was designed to identify and contrast correlations of BOLD signals with choice-relevant SV and choice-irrelevant SV during purchasing and perceptual choices, respectively. It therefore contained the following regressors: first, an indicator function for purchasing choices onsets with three parametric modulators (1, choice-irrelevant FV; 2, choice-relevant SV; 3, price, i.e., the auditory offer number). Second, an indicator function for perceptual choices onsets with three parametric modulators (1, choice-irrelevant SV; 2, choice-relevant FV; 3, auditory offer number). Trial duration in our GLMs was set to the RT on that trial. Each of the regressors was convolved with a canonical hemodynamic response function and regressed against the BOLD signal in each voxel.

The second and third GLMs were estimated to extract parameter estimates from regions of interest that could be used to visualize choice-relevant and choice-irrelevant SV representations (Figures 4E–4H, S1C, and S1D) and to relate brain activity to choice consistency and value-driven attentional capture (see below and Tables S5 and S6). We created five levels of SVs and FVs by partitioning each participant's trials into quintiles (20% bins) based on their individual SV and FV distributions. The onsets of the trials contained in each SV or FV quintile were then entered as indicator functions into the two additional GLMs. The second GLM thus contained five indicator functions for the onsets of purchasing choices corresponding to the choice-relevant SV quintiles and five indicator functions for onsets of perceptual choices contained in the

choice-relevant FV quintiles. The third GLM was identical to the second GLM, but now trials were sorted into quintiles according to the corresponding choice-irrelevant FVs (purchasing choices) and SVs (perceptual choices). A fourth and fifth GLM served as control analyses to test whether price level and price value difference explained any additional variance beyond that of SV in the BOLD signal during purchasing choices (see Supplemental Experimental Procedures and Supplemental Results).

All GLMs modeled MR image auto-correlations with a first-order autoregressive model and also included the following regressors of no interest: 2 indicator functions for purchasing and perceptual block cues, 6 motion parameters (obtained during the realignment procedure), 18 physiological parameters (accounting for cardiac and respiratory fluctuations as well as their interaction), and indicator functions for blinks, saccades, and pupil activity. The last two regressors additionally contained a parametric modulation with saccade size and pupil size, respectively.

First-level summary statistics were obtained by calculating the single-subject voxel-wise contrasts of interest for the SV and FV parametric modulators, both when choice-relevant and choice-irrelevant, as well as their respective interactions. Second-level random-effects group contrast maps were then tested for significance by one-sample t tests on these single-subject contrasts (except for conjunctions, which were tested in a one-way ANOVA). Statistical inference was performed at the cluster level, using a whole-brain FWE-corrected statistical threshold of $p < 0.05$ (based on a cluster-forming voxel cutoff set to $p < 0.001$). For the hypothesis-guided ROI analysis of the VS, we corrected for multiple comparisons using a small-volume correction (SVC; $p < 0.05$) within the bilateral nucleus accumbens volume mask provided by the FSL-Harvard-Oxford-atlas (http://neuro.debian.net/pkgs/fsl-harvard-oxford-atlases.html).

Relating Neural Activity to Behavior

All our analyses relating neural to behavioral measures were performed on data extracted using the LOSO procedure (Esterman et al., 2010), in order to prevent circularity and to ensure unbiased data extraction (Kriegeskorte et al., 2009; Poldrack and Mumford, 2009). The LOSO procedure first uses the data from n-1 subjects to determine the peak activation for a contrast in a given region, and then extracts BOLD signals from a sphere (here of 5-mm radius) around this peak for the independent subject that was not included in the n-1 analysis to determine the ROI. An n-fold replication of this procedure thus ensures that for each subject, the peak coordinates have been determined from an independent sample of participants, thus avoiding double-dipping and selection biases (Kriegeskorte et al., 2009; Poldrack and Mumford, 2009).

In order to relate neural activity to value-based choice consistency, five levels of SVs were created by partitioning each participant's trials into quintiles, identical to the fMRI trial parcellation employed to generate GLM 2 and 3. For each of these SV quintiles, we then computed the proportion of purchasing choices that were SV-consistent. Value-based choices were defined as consistent if a DVD with price $\leq$ SV was purchased or if a DVD with price > SV was not purchased. The fMRI data for these analyses from mPFC and PCC were extracted from ROIs defined with the LOSO approach on the peak of the choice-relevant SV contrast (threshold of $p < 0.0005$ uncorrected), whereas the search space for the VS was confined to the nucleus accumbens volume mask provided by the FSL-Harvard-Oxford-atlas (Figures S1A and S1B).

To test the relationship between these extracted BOLD response profiles and behavior, we performed linear mixed-effects analyses to regress each participant's average purchasing choice consistency for each quintile on the extracted BOLD responses. In these analyses, BOLD responses were treated as fixed effects, and we included intercepts for each participant as random effects. We determined a significant effect of activity in a specific region on behavior by means of a likelihood ratio test of the full model including activity from the region against the null model containing only the intercepts. Additionally, we tested for significant differences in explanatory power between regions by using likelihood ratio tests between full models containing two regions and reduced models with only one region. For instance, to compare the contribution of the mPFC to explaining value-based choice consistency beyond what can be explained by PCC signals, we compared the full model containing fixed effects for mPFC and PCC signals against the reduced model containing only PCC (Table S5; Figure 5A).

To test whether regions that code choice-irrelevant SV are involved in value-driven attentional capture, we used the identical linear mixed-effects analyses procedure as above, except that we now regressed RTs during perceptual choices for each SV quintile on the corresponding SV BOLD responses during perceptual decisions. Individual BOLD response profiles were extracted from spheres (5-mm radius) centered on peaks of the choice-irrelevant SV response, independently determined using the LOSO procedure on the choice-irrelevant SV contrast (threshold of $p < 0.0005$ uncorrected) for PCC, bilateral dlPFC, and bilateral parietal lobule (Table S6; Figure 5C).

In order to test whether trial-wise signals in the mPFC, VS, and PCC also differ in their capability of predicting actual purchases, we extracted BOLD time series for each subject, session, and ROI using LOSO as above (restricted to the choice-relevant SV contrast), and transformed them to percent signal change. To increase precision with respect to trial onset, the average time course for each region was interpolated to 100-ms intervals using a cubic spline. We quantified the reliability with which the single-trial amplitude of the BOLD signal predicted actual purchasing choices (purchasing versus not purchasing) using an ROC analysis (Green and Swets, 1966), conducted at each 100-ms time point within the period of 1 s before to 13 s after the onset of a trial (Figure 5B). The area under the ROC (AUC) provides a measure of the separability of two conditions and can be used to test the statistical significance of the purchasing/not purchasing prediction from the BOLD data. AUC is widely employed for quantification of categorical predictions, for instance in single cell (Reddy et al., 2006), EEG (O'Connell et al., 2012), or fMRI data (Skudlarski et al., 1999; Sorenson and Wang, 1996).

To estimate and compare the predictive power of BOLD signals in different ROIs for purchases, we estimated the Z statistic for each ROI, subject, and time point. To this end, we first generated the null distribution of the AUC curve for chance performance AUC_{chance} via 1,000 iterations of randomly shuffled trial labels while conserving the individual proportions of purchase/not purchase decisions. These computations were implemented independently for each time point t. For each ROI and subject, the individual Z statistic Z_t was then computed at each time point t using the following formula:

$$Z_t = \frac{AUC_t - \mu_{AUC_{t\ chance}}}{\sigma_{AUC_{t\ chance}}}$$

$\mu_{AUC_{t\ chance}}$ represents the mean AUC of the 1,000 randomizations, and $\sigma_{AUC_{t\ chance}}$ represents the SD of the 1,000 randomizations. For each region, the average across subjects at each time point t yielded the group Z statistic at that time point. This index yields above-chance purchase predictability when the group Z statistic exceeds the critical value of 1.64, corresponding to a significance level of $p < 0.05$ one-tailed (please note that identical results are observed using the corresponding two-tailed significance threshold, $Z > 1.96$). Group Z statistic comparisons between ROIs were conducted at each time point t using a paired t test. This analysis allowed us to statistically examine whether we can predict a purchasing decision on a single-trial basis.

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures, six tables, Supplemental Experimental Procedures, and Supplemental Results and can be found with this article online at http://dx.doi.org/10.1016/j.neuron.2014.12.054.

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